

Part I: The locality of Tiupampa: age, taphonomy and mammalian fauna

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ABSTRACT

The specimens of *Pucadelphys andinus* studied in this volume were collected in the early Paleocene beds of the Santa Lucía Formation at Tiupampa (Bolivia). In this first part, a short presentation is given of the locality of Tiupampa, of the horizon from which the skeletons of *Pucadelphys andinus* were collected and of their age. We also provide an updated list of the mammalian fauna yielded by the site, and present comments on the taphonomy and paleoenvironment of the oldest known undoubted marsupial skeletons.

RÉSUMÉ

Première partie : le gisement de Tiupampa : âge, taphonomie et faune de mammifères

Les spécimens de *Pucadelphys andinus* qui font l'objet de ce mémoire ont été récoltés dans des niveaux du Paléocène ancien de la Formation Santa Lucía à Tiupampa (Bolivie). Cette première partie offre une brève présentation de la localité de Tiupampa, de l'horizon d'où proviennent les squelettes et de leur âge. Elle contient aussi une liste mise à jour de la faune mammalienne d'accompagnement, ainsi que des informations sur la taphonomie et le paléoenvironnement de ces squelettes de marsupiaux, qui sont les plus anciens actuellement connus.

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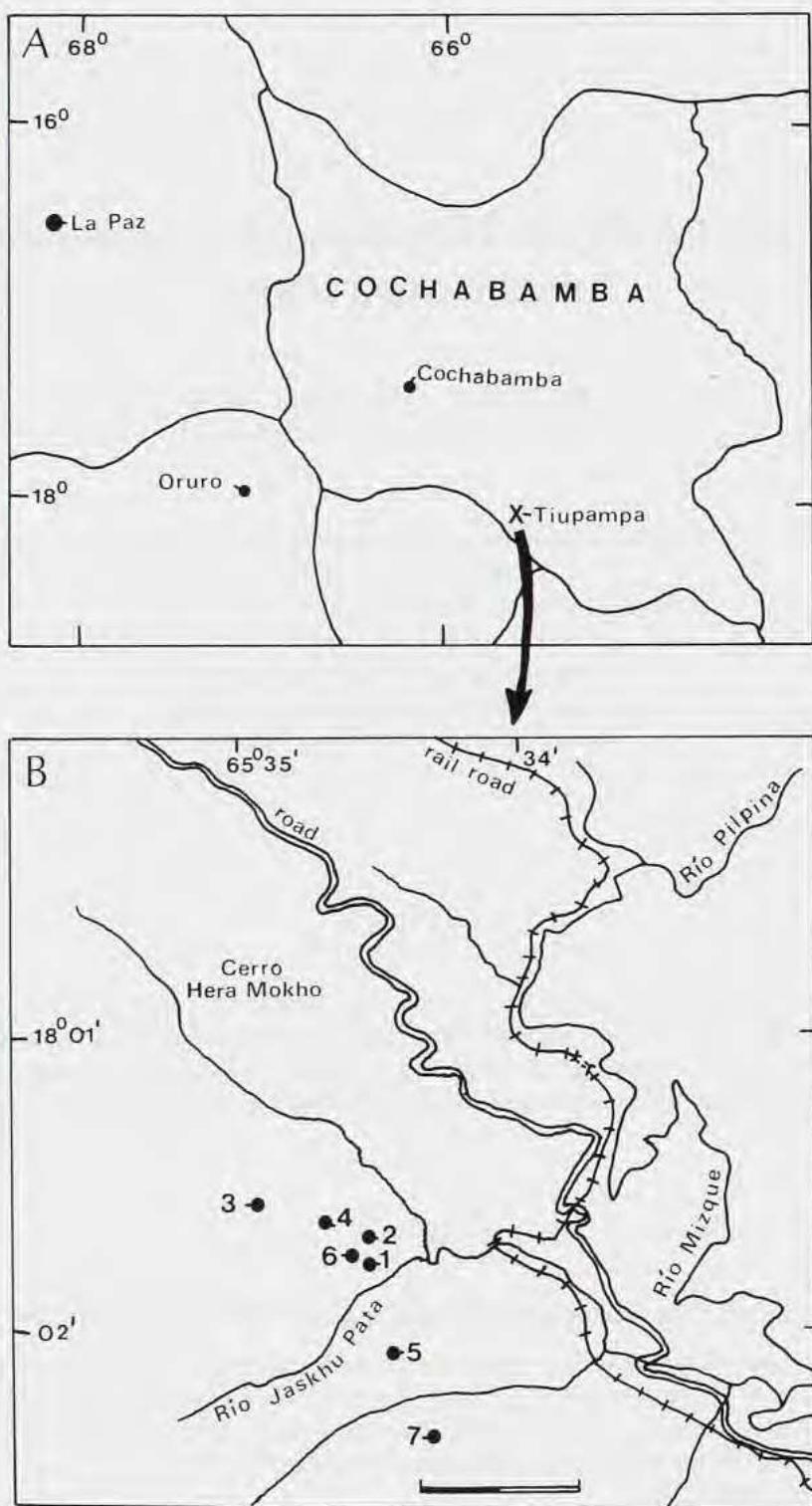


FIG. 1. — Map of southcentral Bolivia showing location of Tiupampa (top) and detail map of Tiupampa area showing fossil vertebrate sites (bottom). The skeletons of *Pucadelphys andinus* are from site 1 ("the quarry").

FIG. 1. — Carte de la partie sud du centre de la Bolivie montrant la situation de Tiupampa (en haut), et carte détaillée de la région de Tiupampa montrant les localités à vertébrés fossiles (en bas). Les squelettes de *Pucadelphys andinus* proviennent de la localité 1 ("the quarry").

The locality of Tiupampa, recognized as a promising site as early as 1980 by R. HOFFSTETER, C. DE MUIZON and P. TAQUET, yielded its first mammalian remains (a marsupial) during a second campaign (1982) organized in particular by L. G. MARSHALL and Ch. DE MUIZON. It was in the course of a 4th campaign (1985) that the skeletons of *Pucadelphys andinus* presented here were found.

LOCALITY, HORIZON, AND AGE

These specimens were recovered from the Santa Lucía Formation (*sensu* GAYET *et al.*, 1992; MUIZON, 1992; MUIZON & BRITO, 1993) at Tiupampa, located about 95km southeast of Cochabamba (65°35'W, 18°02'S), Mizque Province, Department of Cochabamba, southcentral Bolivia (Fig. 1, top). Details of the topography are shown on Carta Nacional Boliviana San Vicente Quadrangle, Hoja 6439 I, serie H731, I/50,000, 1968. All specimens are from site 1 ("the quarry") (Fig. 1, bottom).

The rich and taxonomically diverse vertebrate fauna discovered at Tiupampa in 1982 was initially believed to be from the "Late Cretaceous" age El Molino Formation (MARSHALL *et al.*, 1983; 1985; MUIZON *et al.*, 1983, 1984; MARSHALL & MUIZON, 1988). However, recent detailed studies of the biostratigraphy (GAYET *et al.*, 1992) and stratigraphy (SEMPERE, 1994) of the El Molino and overlying Santa Lucía Formations reveal the following: 1) uncontested Late Cretaceous age "guide" fossils (i.e. dinosaurs, some selachians and fish) occur only in the lower and basal middle members of the El Molino Formation, which collectively span early and late Maastrichtian times; 2) the upper member of the El Molino Formation is Early Paleocene (Danian); 3) the K/T boundary lies in the upper part of the middle member of the El Molino Formation; but, another interpretation is given by JAILLARD *et al.* (1993: 650) who definitely consider the El Molino Formation as a lateral equivalent of the Upper Vilquechico Formation from Peru, which they ascribed to a latest Campanian-late Maastrichtian interval (JAILLARD *et al.*, 1993: 655). The mammal-bearing level at Tiupampa, which has yielded the type fauna of the Tiupampian Land Mammal age, has been assigned to the Santa Lucía Formation (GAYET *et al.*, 1992; MUIZON, 1992; and MUIZON & BRITO, 1993) and has been given an early Paleocene age (ORTIZ JAUREGUIZAR & PASCUAL, 1989; MARSHALL, 1989; BONAPARTE *et al.*, 1993; MUIZON & BRITO, 1993). Finally, studies in progress on the geochronology of the El Molino and Santa Lucía Formations (SEMPÈRE & MARSHALL, in prep.; SEMPÈRE *et al.*, in prep.) would suggest an age slightly younger in the Paleocene than stated before. Pending formal publication of these results, the Tiupampa land mammal fauna and the Tiupampian land-Mammal age will be referred here to the early Paleocene following VAN VALEN (1988), MUIZON (1992), BONAPARTE *et al.* (1993), and MUIZON & BRITO (1993).

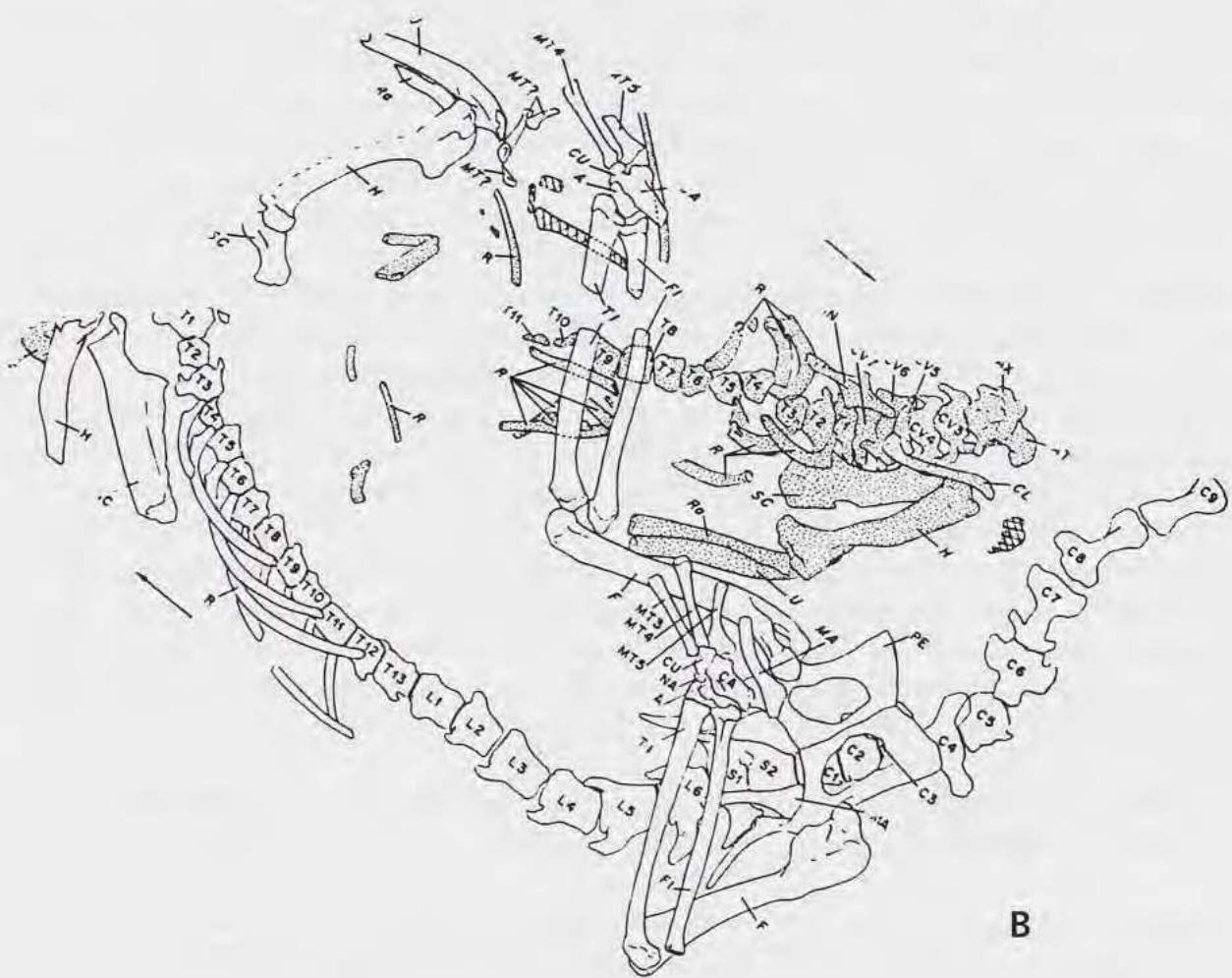
Stratigraphic sections showing the location of the fossil level in the Tiupampa section are provided by MUIZON *et al.* (1983, fig. 1) and MARSHALL *et al.* (1985, fig. 4, right).

TAPHONOMY

The Santa Lucía Formation at Tiupampa was deposited in channels of meandering rivers on a flat alluvial plain. The water-lain sediments surrounding the skeletons are a well-sorted, weakly



A



B

consolidated, fine-grained quartzose-sandstone with sparse feldspar grains, some hematite and traces of red clay between the predominantly quartz grains. The red color comes from the iron dioxide. The presence of several taxa of crocodiles attests to a warm, probably subtropical, climate.

The specimens were collected from sediment blocks that had been transported about 2km from site 1 (Fig. 1, bottom) to a screen-washing location; they were first observed by P.-Y. GAGNIER. The blocks containing the skeletal remains were prepared at the MNHN by C. DE MUZON and L. G. MARSHALL. This revealed that four partial skeletons were represented and that these occurred in pairs (6105 and 6106, 6110 and 6111, respectively; see below).

The individuals of each pair were apparently in a “snuggle” position and facing in opposite directions (Figs 3 and 4). We interpret this relationship to indicate that these animal-pairs (probably male and female, see below) were in burrow-nests and sleeping (or resting) in a snout-rump position typical of many living didelphids (see below). We further believe that these animals probably died as the result of a flood that entrapped them in their burrows and filled the latter with water and sediment. The “died-in-a-burrow” hypothesis is supported by the fact that frogs (some represented by complete skeletons, BAEZ, 1992) are abundant throughout “the quarry” fossil level, and that these apparently lived in a pond or oxbow adjacent to a bank that was used as a burrow-nest site; this interpretation would also explain the exceptionnally high number of fossils in this level, which may have died as a result of a single catastrophic flood (SEMPERE & MARSHALL, in prep.).

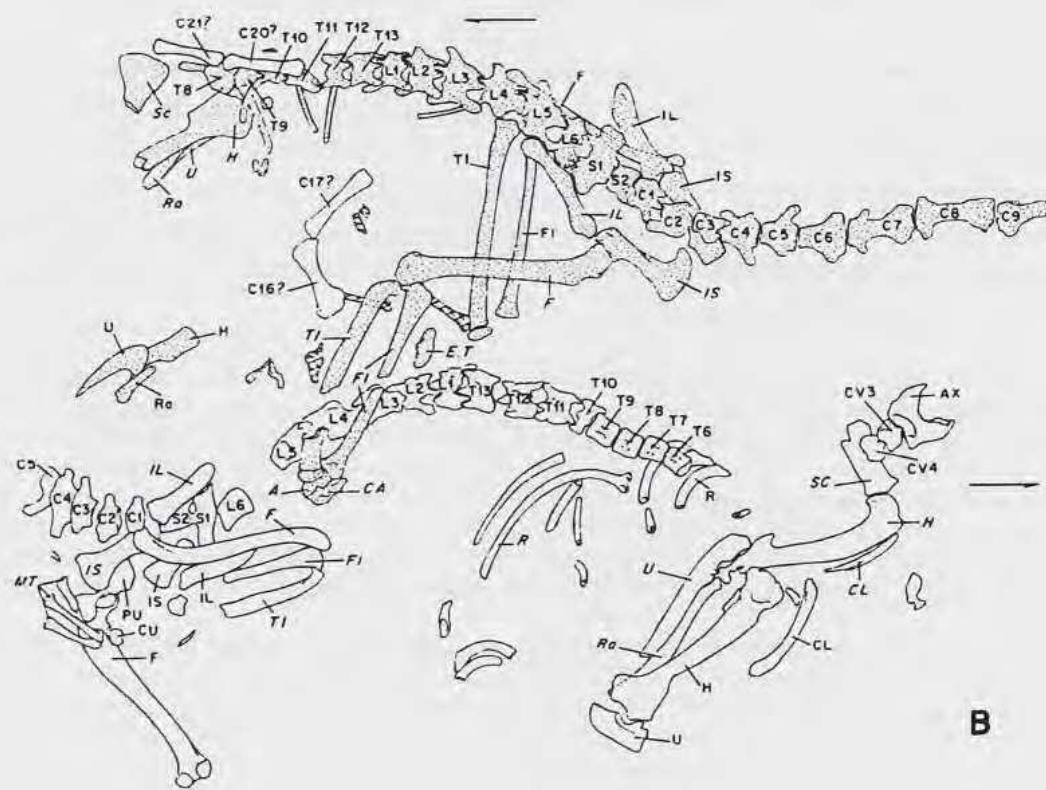
There was apparently little time lapse between death and the onset of fossilization (*i.e.* permanent entombment in the sediment). This is evidenced by the fact that the majority of bones are articulated, suggesting little or no postmortem dismemberment. Nevertheless, some rib fragments in both specimen-pairs are situated “out-of-context” of the main skeletons, no distal phalanges or claws are articulated with the four partial pes and only five caudal vertebrae posterior to C9 are preserved. These features are interpreted to indicate that some movement of sediment

FIG. 2. — *Pucadelphys andinus*. A, specimen-pair YPFB Pal 6105, holotype, (top) and YPFB Pal 6106 (bottom) photographed at initial stage of preparation; 6105 faces right; 6106 faces left. X3/4. B, line-drawing of same specimen-pair after preparation (skull of YPFB Pal 6105 detached). Bones of YPFB Pal 6105 are stippled and bones of YPFB Pal 6106 are left white to facilitate identification and association. X 1,5. In Roman letters, unpaired bones and paired bones of the right side; in italics, paired bones of the left side; cross-hatched, unattributed bones. Abbreviations: A, astragalus; AT, atlas; AX, axis; C, caudal vertebra; CA, calcaneum; CL, clavicle; CU, cuboid; CV, cervical vertebra; F, femur; FI, fibula; H, humerus; IL, ilium; IN, interclavicle; IS, ischium; L, lumbar vertebra; MA, os marsupium; MT, metatarsal; NA, navicular; PU, pubis; R, rib; RA, radius; S, sacral vertebra; SC, scapula; T, thoracic vertebra; TI, tibia; U, ulna.

FIG. 2. — *Pucadelphys andinus*. A, couple de spécimens (YPFB Pal 6105, holotype, en haut) et YPFB Pal 6106 (en bas) photographiés au début de la préparation: YPFB Pal 6105 est sur le côté droit, 6106 sur le côté gauche. X 3/4. B, dessin au trait des mêmes spécimens après préparation (le crâne de YPFB Pal 6105 a été retiré). X 1,5. Les os de YPFB Pal 6105 sont pointillés et ceux de YPFB Pal 6106 ont été laissés en blanc pour faciliter l'identification et les associations. En lettres romaines, os impairs et os pairs du côté droit; en italiques, os pairs du côté gauche; en hachures, os non attribués. Abréviations: A, astragale; AT, atlas; AX, axis; C, vertèbre caudale; CA, calcanéum; CL, clavicule; CU, cuboïde; CV, vertèbre cervicale; F, fémur; FI, fibula; H, humérus; IL, ilion; IN, interclavicule; IS, ischium; L, vertèbre lombaire; MA, os marsupial; MT, métatarsien; NA, naviculaire; PU, pubis; R, côte; RA, radius; S, vertèbre sacrée; SC, scapula; T, vertèbre thoracique; TI, tibia; U, cubitus.



A



B

around the corpses occurred, causing minor displacement and/or loss of some fragile extremity bone elements. Diagenetic processes were, however, exceedingly weak as evidenced by the facts that the sediments are poorly consolidated, the bones show no or only minor evidence of deformation, and the skulls and skeletons are preserved in a three dimensional, "life-like" state.

MAMMALIAN FAUNAL LIST

The Locality of Tiupampa has yielded an abundant mammalian fauna. An updated list (modified from MUIZON, 1992 and MUIZON & BRITO, 1993) is given below:

Class Mammalia

Infra-class Metatheria

Order Sparassodonta

Family Hathliacynidae

Allqokirus australis Marshall & Muizon, 1988

Family Mayulestidae

Mayulestes ferox Muizon, 1994

Order Peralectria

Family Peralectidae

Peralectes cf. austrinum

Roberthoffstetteria nationalgeographica

Marshall, Muizon & Sigé, 1983

Order Microbiotheria

Family Microbiotheriidae

Khasia cordillerensis Marshall & Muizon, 1988

FIG. 3.—*Pucadelphys andinus*. A, specimen-pair YPFB Pal 6110 (bottom) and YFPB Pal 6111 (top) photographed at initial stage of preparation. YPFB Pal 6110 faces right; YPFB Pal 6111 faces left. X 3/4. B, line drawing of same specimen-pair after preparation (skull of YPFB Pal 6110 detached). X 1.5. Bones of YPFB Pal 6111 are stippled and bones of YPFB Pal 6110 are left white to facilitate identification and association. In Roman letters, unpaired and paired bones of the right side; in italics, paired bones of the left side; cross-hatched, unattributed bones. In the part of YPFB Pal 6110 corresponding to Fig. 4, bones are drawn reversed. For abbreviations, see caption to Fig. 2.

FIG. 3.—*Pucadelphys andinus*. A, couple de spécimens YPFB Pal 6110 (en bas) et YFPB Pal 6111 (en haut) photographiés au début de la préparation. YPFB Pal 6110 est sur le côté droit; YFPB Pal 6111 sur le côté gauche. X 3/4; B, dessin au trait des mêmes spécimens après préparation (le crâne de YPFB Pal 6110 a été retiré). X 1.5. Les os de YFPB Pal 6111 sont pointillés et ceux de YPFB Pal 6110 ont été laissés en blanc pour faciliter l'identification et les associations. En lettres romaines, os impairs et os pairs du côté droit; en italiques, os pairs du côté gauche; en hachures, os non attribués. Sur la partie de YPFB Pal 6110 correspondant à la Fig. 4, le dessin a été renversé. Pour les abréviations, voir légende Fig. 2.

- Order Didelphimorphia
 - Family Didelphidae
 - Pucadelphys andinus* Marshall & Muizon, 1988
 - Incadelphys antiquus* Marshall & Muizon, 1988
 - Mizquedelphys pilpinensis* Marshall & Muizon, 1988
 - Andinodelphys cochabambensis* Marshall & Muizon, 1988
 - Tiulordia floresi* Marshall & Muizon, 1988
 - Family Jaskhadelphydae
 - Jaskhadelphys minutus* Marshall & Muizon, 1988
- Infra-class Eutheria
 - Order Leptictida
 - Family Palaeoryctidae?
 - cf. *Cimolestes* sp.
 - Family indet.
 - Gen. and sp. indet.
 - Order Pantodonta
 - Family Alcidedorbignyidae
 - Alcidedorbignya inopinata* Muizon & Marshall, 1987
 - Order Condylarthra
 - Family Mioclaenidae
 - Molinodus suarezi* Muizon & Marshall, 1987
 - Tiuclaenus minutus* Muizon & Marshall, 1987
 - Tiuclaenus* sp. nov. 1
 - Tiuclaenus* sp. nov. 2
 - Pucanodus gagnieri* Muizon & Marshall, 1991
 - Mioclaenidae nov. gen., nov. sp.
 - Family Mioclaenidae or Didolodontidae
 - Andinodus boliviensis* Muizon & Marshall, 1987
 - Family ?Peritychidae
 - aff. ?*Mimatuta*
 - Order Condylarthra *incertae sedis*
 - Family Kollpaniidae
 - Kollpania tiupampina* Marshall & Muizon, 1988
 - Order Notoungulata
 - Family Henricosborniidae or Oldfieldthomasiidae

ABBREVIATIONS OF INSTITUTIONS

MNHN, Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France.
 YPFB Pal, Paleontology collection of Yacimientos Petrolíferos Fiscales de Bolivia in the Centro de Tecnología Petrolera, Santa Cruz, Bolivia.



FIG. 4.—*Pucadelphys andinus*. YPFB Pal 6110, reversed photo (X 3) of accessory block, to show its continuity with main block in Fig. 3 (see explanation Fig. 26).

FIG. 4.—*Pucadelphys andinus*. YPFB Pal 6110, photo renversée (X3) du bloc accessoire, pour montrer la continuité avec le bloc principal de la Fig. 3 (voir explication Fig. 26).

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